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A new fossil species of *Cryptomeria* (Cupressaceae) from the Rupelian of the Lühe Basin, Yunnan, East Asia: Implications for palaeobiogeography and palaeoecology

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ABSTRACT

Cryptomeria (Cupressaceae) is a relic genus that was widely distributed throughout Eurasia during the Cenozoic. Interpretation of the biogeographic history of this genus is currently limited by lack of fossil records from the Paleogene of East Asia. Here, we report on a new fossil species of *Cryptomeria*, *Cryptomeria yunnanensis* W.N. Ding et Z.K. Zhou sp. nov., based on well-preserved compressions and impressions from the Rupelian (~32 Ma) of the Lühe Basin, Yunnan, Southwest China. Sterile shoots are assigned to *Cryptomeria* based on gross-morphological and cuticular (morphological) characters and are compared with extant and fossils species described so far. The shoots exhibit spirally arranged sessile subulate leaves, leaf cuticles show densely arranged and irregularly oriented monocyclic stomata, which are characteristic for the genus. Contemporary and historical distributions of *Cryptomeria* suggest that a decrease of precipitation in former distribution areas in East Asia may have been crucial in shaping the present relic distribution pattern of this ancient conifer.

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1. Introduction

Cenozoic plant relics include species that were once widespread in the geological past but are now restricted to rather small isolated areas as a result of environmental and climate changes (Milne and Abbott, 2002; Manchester et al., 2009; Huang et al., 2015). Plant relics and their fossil ancestors provide valuable information on how plants have responded to climate change because their modern climate requirements are fully understood (Huang et al., 2015). *Cryptomeria* (Cupressaceae) is a relic genus with only one extant species, *Cryptomeria japonica*. Natural forests with native stands of *C. japonica* var. *japonica* are limited to Japan (Nishida and Uemura, 1997; Fu et al., 1999). *Cryptomeria japonica* var. *sinensis* is native in China with a few occurrences in Fujian (Nanping), Jiangxi (Mt. Lu shan), Sichuan, Yunnan, Zhejiang (Mt. Tianmu shan) but wild populations are hardly to distinguish from an enormous number of cultivated stands in central and southern China (Fu et al., 1999).

However, fossil records indicate that during the Cenozoic *Cryptomeria* was once widely distributed throughout Eurasia. Therefore, *Cryptomeria* is a promising example to elucidate the evolutionary history of relic plants in response to climatic and environmental changes by disentangling its biogeography throughout the geological past.

The earliest fossil record of *Cryptomeria* was described based on vegetative organs from the Paleogene in Kamchatka, Far East of Russia (Chelebaeva, 1991; Budantsev, 1997). For the Neogene, *Cryptomeria* is well represented in the fossil records of Europe and Japan, including seed cones, leafy shoots and wood (Kilpper, 1968; Mai and Walther, 1988; Momohara, 1992; Mai, 1997; Nishida and Uemura, 1997; Barrón, 1998; Denk et al., 2005; Dolezych and Schneider, 2006; Yabe, 2008; Manchester et al., 2009; Barrón et al., 2014). Living *Cryptomeria japonica* shows a relic distribution after the demise of the European fossil representatives. However, no confirmed fossil record of *Cryptomeria* has been reported so far within its extant distribution area in southern China. Owing to the limited regional fossil record, little is known how *Cryptomeria* became restricted to its present refuge in China. Therefore, the new fossil record from southwestern China is important for interpreting the extant biogeographical pattern of *Cryptomeria*.

In this study, we report a new fossil species of *Cryptomeria* based on well-preserved leafy shoots collected from the Rupelian (32 ± 1 Ma: Linnemann et al., Submitted for publication) lacustrine deposits in Lühe, Yunnan Province, southwestern China. We identified the fossils

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as *Cryptomeria* based on their macromorphology and cuticular micromorphology. Furthermore, we discuss how its palaeobiogeographic history corresponds to climatic changes in the Cenozoic.

2. Material and methods

2.1. Geological setting

Fossil samples were collected from the Lühe Basin, Nanhua County, Yunnan Province, southwestern China (25°8.5′ N, 101°22.5′ E, 1, 882 m a.s.l.; Fig. 1). The fossil-bearing profile was exposed by recent construction work in Lühe Town (Fig. 1A). In the basin, Rupelian fossiliferous lacustrine deposits, superimposed on Cretaceous purple-red silty mudstones, are overlain by a Quaternary laterite (Zhang, 1996). The fossiliferous lacustrine deposits of the study site are composed of siliciclastic sediments and several volcanic ash layers (Fig. 2). These are in ascending order (1) conglomerates and breccias, (2) silty mudstones intercalated by thin coal beds, (3) carbonaceous mudstones intercalated by tuffaceous layers, and (4) silty mudstones yielding *Cryptomeria* fossils (Fig. 2). In the upper part of the section, the sediments are oxidized. *Cryptomeria* fossils were collected both from oxidized and non-oxidized sediments. Thus, compression fossils with cuticles were obtained from non-oxidized sediments, whereas oxidized sediments yielded only impressions.

The lacustrine section was correlated to the adjacent lignite-bearing section of the late Miocene to early Pliocene age in Lühe Coal Mine (Zhang, 1996; Yi et al., 2003; Ma et al., 2005; Zhang et al., 2007; Xu et al., 2008). Recent U—Pb zircon dating of the three lowermost volcanic ash layers yielded a rather distinct age, uniformly c. 32 ± 1 Ma (Linnemann et al., Submitted for publication). This is regarded as the age of the lacustrine sequence including the fossil-bearing strata of the site in Lühe Town. This is also the minimum age of zircon populations in fluvial units within the coalmine reported by Wissink et al. (2016), which supports the correlation between the Lühe Town section and that exposed in the nearby coalmine.

2.2. Methods

Seven sterile leafy shoot specimens were available for this study; three specimens are compressions and four are impressions. Photographs were taken using a digital camera (Nikon D700). Detailed structures of these specimens were observed and photographed using a stereoscope microscope (Leica S8AP0).

To obtain leaf cuticles, several pieces of fossil material were treated with Schulze's solution, neutralized with 5% KOH and washed with distilled water. The cuticles were stained with Safranin and embedded in glycerin jelly to prepare slides for microscopic analysis following the methods by Kerp (1990). Epidermal characters were observed using a stereomicroscope (Leica DM750) and photographed using a scanning electron microscope (Zeiss EVOLS10).

The morphometric study was conducted using Image J Version 1.47 (http://rsb.info.nih.gov.ig/). Line-drawings of the fossil specimens were created using CorelDraw X7. The geographic distributions of modern *Cryptomeria* were plotted using software ArcGIS 9.3 and CorelDraw X7. The occurrences of extant *Cryptomeria* were collected from previous publications (Tsukada, 1982, 1986) and Chinese Virtual Herbarium (CVH) Data Portal (www.cvh.org.cn). The fossil record of *Cryptomeria* was compiled from publications and online databases, e.g., http://www.fossil-cad.net/index2.html (Xing et al., 2016). Fossils were compared with extant *Cryptomeria japonica* and other morphologically similar taxa, i.e. *Araucaria cunninghamii*, *Glyptostrobus pensilis*, *Taiwania cryptomerioides* and *Taxodium distichum*. Material of extant species was collected at Kunming Institute of Botany and Xishuangbanna Tropical Botanical Garden.

3. Systematics

Family — Cupressaceae Gray 1822

Genus — *Cryptomeria* D. Don 1838

Species — *Cryptomeria yunnanensis* W.N. Ding et Z.K. Zhou sp. nov. (Plates I–III).

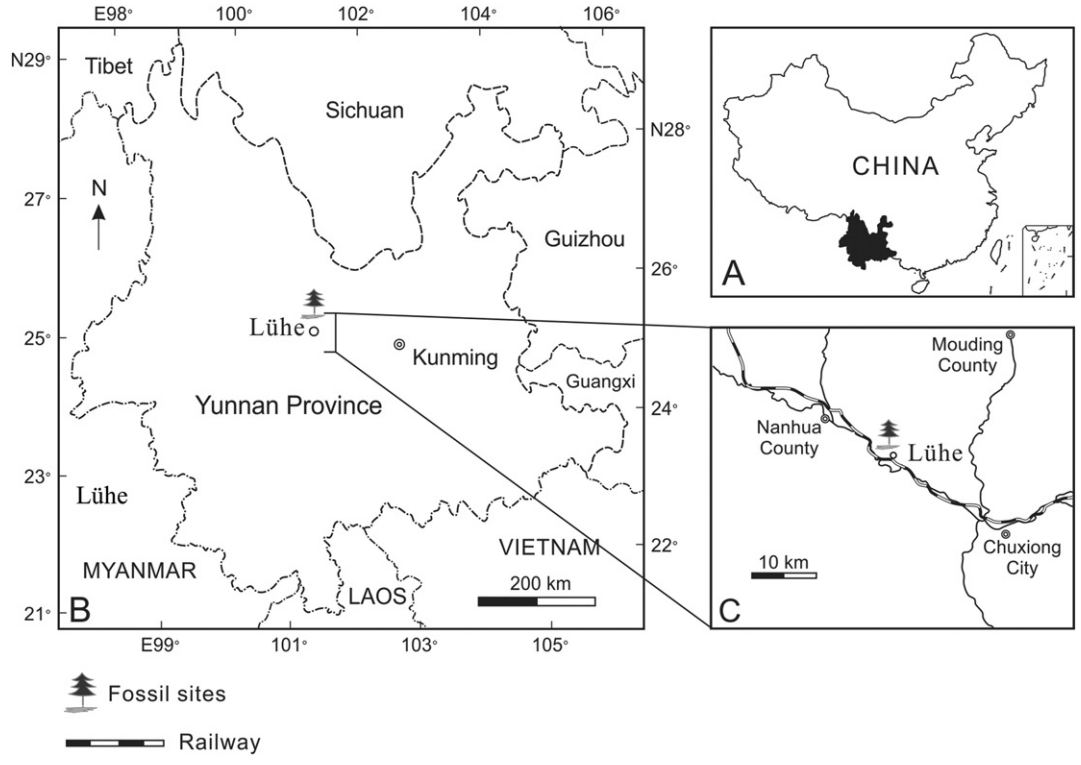

Fig. 1. The fossil locality of this study in central Yunnan, SW China.

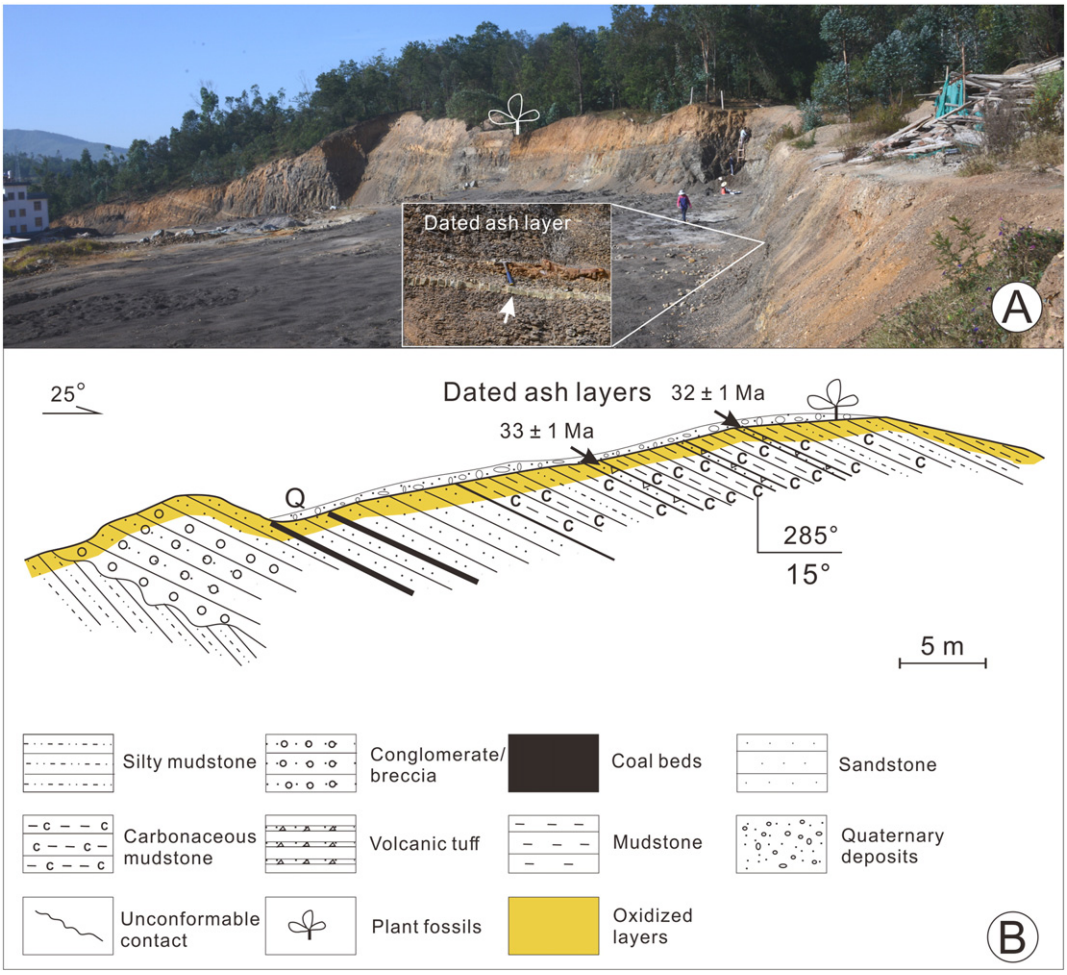

Fig. 2. Geological cross section of the outcrop in Lühe Town, central Yunnan, SW China.

Specific epithet — The specific name, *yunnanensis*, is derived from Yunnan, a province in southwestern China where the fossil site is located.

Holotype — KUN PCLH2-0255 (A, B) (Plate I, 1, 4).

Paratypes — KUN PCLH2-0059 (Plate I, 2), KUN PCLH1-0344 (A, B) (Plate II, 9–10), KUN PCLH1-0353 (A, B) (Plate II, 1–3, 5–7).

Repository — The Herbarium of Kunming Institute of Botany (KUN), Chinese Academy of Sciences.

Type locality — Lühe Town, Nanhua County, Yunnan Province, China.

Age — Rupelian (c. 32 ± 1 Ma).

Diagnosis — Leafy twigs, spirally arranged sessile subulate leaves with a decurrent base, apices acute and sometimes incurved. Adaxial and abaxial surfaces convex, lateral surfaces keeled. Stomata monocyclic, densely arranged and irregularly oriented, oval to roundish, with a simple circle of subsidiary cells bordered by faintly thicker anticlinal walls.

Descriptions — Leafy shoots are 17.9–76.7 mm long and 2.3–9.3 mm wide. The expanded leaves are attached helically to the shoot axis (Plate II, 1, 5). Leaves are subulate in shape, broadest at the base, and they tend to be straight or incurved in the apical part (Plates I, 1–4; II, 2–3, 6–7). Arising from the rachis at angles of 20–60°, leaves overlap along the shoot axis (Plates I, 1–4; II, 1–3, 5–7). The apex is acute, and the base is decurrent. Adaxial and abaxial surfaces are convex (Plate II, 3). The lateral leaf surfaces are visibly keeled as a slightly sinuous line running parallel with and close to the adaxial edge of the leaves (Plate II, 7). Leaves of specimen KUN PCLH1–0344 have a scattered arrangement and diverge with wider angles from the axis (Plate II, 9–10). Leaves are 1.6–6.2 mm long and 0.8–2.1 mm wide; their length to width ratio is 1.5–4.4.

Cuticles are fragmented but robust. Stomatal bands, as well as several non-stomatal zones are visible on both abaxial and adaxial surfaces of the leaf (Plate III, 1–3). The epidermal cells on both surfaces are similar in shape and size (Plate III, 1–2). Ordinary epidermal cells of the non-stomatal zones are elliptic, rectangular, quadrangular or spindle-shaped (Plate III, 1–2, 7), and they are 27.5–63.2 μm long and 10.0–27.3 μm wide; their length to width ratio is 0.6–5.3. Epidermal cells form regular ranks, and their anticlinal walls are straight (or slightly wavy) and thick (Plate III, 7–9). Epidermal cells between stomata are irregularly shaped and arranged in comparison with those of non-stomatal areas (Plate III, 1–4). The epidermal cells on the leaf margin are rectangular in shape and obliquely oriented to the ordinary epidermal cell rows (Plate III, 1, 3).

Bands of stomata are aligned parallel to the midrib and the leaf margin; stomata are predominantly densely and randomly arranged within bands. The orientation of stomatal pores relative to the leaf midvein is random (Plate III, 1–3). The outline of the stomatal complexes is oval to roundish, 40.0–73.4 μm long and 34.2–63.5 μm wide; having a length to width ratio of 0.7–1.9 (Table 3). Stomatal complexes are monocyclic. Guard cells are sunken, and periclinal walls are 7.4–8.9 μm thick, especially on outer margins. (Plate III, 7–9). Four to six subsidiary cells are quadrilateral overarching parts of the guard cells. The outer anticlinal walls of the subsidiary cells have a thicker flange of cutin than those of the ordinary epidermal cells (Plate III, 7–9).

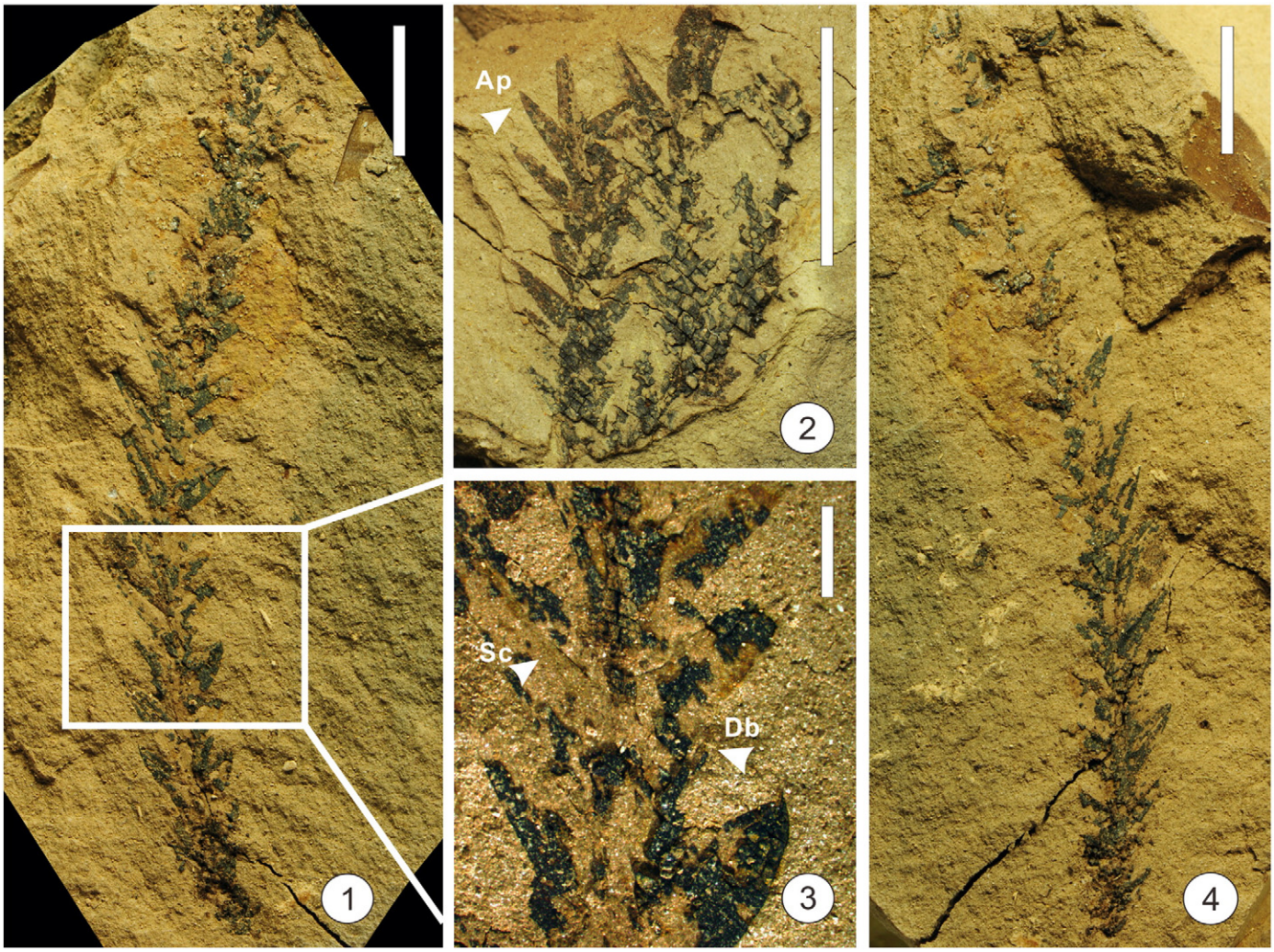

Plate I. *Cryptomeria yunnanensis* sp. nov. compression material. 1 and 4. Holotype and its counterpart; leafy shoot with cuticles. Specimen KUN PCLH2-0255. Bar = 1 cm. 2. Paratype. Specimen KUN PCLH2-0059. The arrow indicates the acute apex (Ap). Bar = 1 cm. 3. Enlargement of the leafy shoot, showing spirally arranged subulate leaves, and decurrent base (Db), adaxial and abaxial surfaces convex (Sc). Bar = 5 mm.

4. Discussion

4.1. Assignment to Cryptomeria

The Lühe material shows morphological similarities to extant genera, including *Araucaria*, *Cryptomeria*, *Glyptostrobus*, *Taiwania* and *Taxodium* (Plate IV, 1, 5, 9; Table 2). The fossil material has a similar leaf shape to *Taiwania* but differ in epidermal features such as stomatal type and arrangement (Table 2). In our fossils, stomata are densely arranged and irregularly oriented, oval to roundish in outline, and epidermal cells between stomata are irregularly arranged (Plate III, 1–4). In *Taiwania*, the stomatal pores are mostly oriented parallel to the leaf midvein and stomata are usually rectangular to elongate in shape (Plate IV, 6–8). Our fossils differ from *Araucaria*, in that the latter has ordinary epidermal cells with conspicuous undulating anticlinal walls, and stomata are usually arranged in regular rows with the polar cells oriented in the same direction (Plate IV, 10–12) (Stockey and Taylor, 1978; Stockey and Ko, 1986).

The fossil material is distinguished from *Taxodium* and *Glyptostrobus* by having subulate leaves with convex on adaxial and abaxial surfaces. The subulate leaves of our fossils are straight or inwardly curved, but they are outwardly curved in *Taxodium* and *Glyptostrobus*. Our fossils also show differences in cuticular micromorphology (Table 2). The stomata are monocyclic and the outer anticlinal walls of the subsidiary cells have distinct thickenings in comparison to those from the ordinary epidermal cells. However, subsidiary cells of adjacent stomatal complexes are sometimes shared as in *Taxodium* (Ma et al., 2004b; Kunzmann et al., 2009). In our specimens, the long axes of the stomatal pores are randomly oriented with respect to the midvein, and the group of subsidiary cells surrounding each stoma exhibits a very distinctive oval to roundish appearance on the inner surface of the cuticle. In *Glyptostrobus*, the long axes of stomatal pores are mostly parallel to the midvein in linear-subulate leaves (Ma et al., 2004a), and so are distinguishable from those of our specimens.

Our specimens from Lühe undoubtedly belong to the genus *Cryptomeria* based on the following characters: (1) Leafy twigs bearing spirally and densely arranged subulate leaves (Plates I and II); (2) leaves sessile, base decurrent, apex acute and straight or incurved (Plate II, 1–3); (3) adaxial and abaxial surfaces convex, lateral surfaces keeled indicated as a line running parallel with and close to the adaxial edge of leaves (Plates I, 1–4; II, 1–3, 6); (4) leaves are amphistomatic (Plate III, 2); and (5) stomata monocyclic, irregularly oriented, oval to roundish in outline with four to six subsidiary cells (Plate III,1–7).

4.2. Comparison with fossil Cryptomeria species and extant Cryptomeria japonica

Currently, seven fossil species of *Cryptomeria* have been documented from Eurasia (Table 1). *Cryptomeria rhenana* and *C.* cf. *rhenana* Kilpper

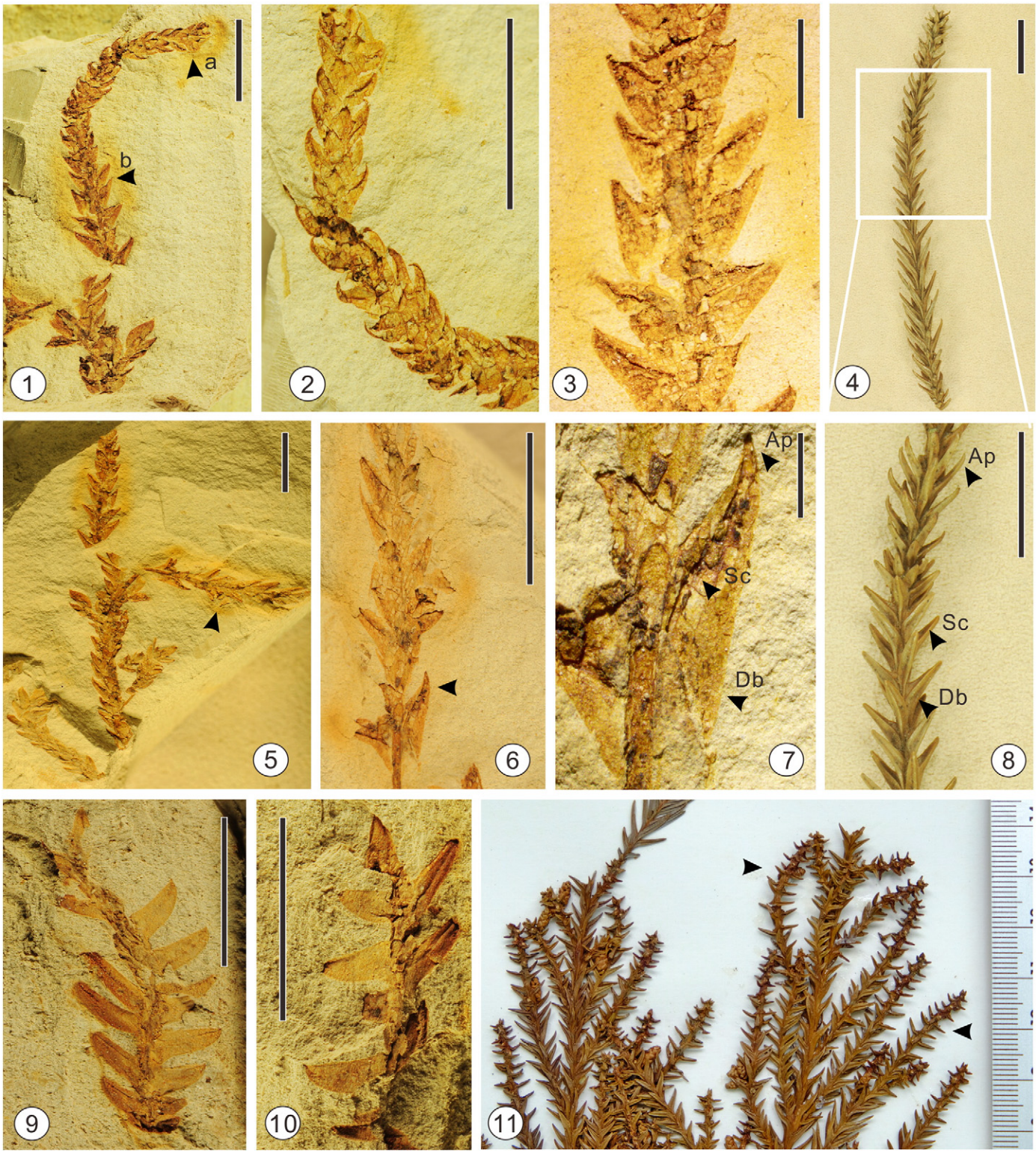

Plate II. *Cryptomeria yunnanensis* sp. nov. impression material (1–3, 5–7, 9–10) and extant *Cryptomeria japonica* (Thunb. ex L. f.) D. Don. (4, 8 and 11). 1–3. Leafy twigs bearing spirally arranged sessile subulate leaves with decurrent base. Specimen KUN PCLH1-0353. Bar = 1 cm. 2. Enlargement of leafy twig (arrow a). 3. Enlargement of leafy twig (arrow b), showing leaves tend to be straight or incurved at apex. 5–7. Leafy twigs from the counterpart of KUN PCLH1-0353. Bar = 1 cm. 6. Enlargement of the leafy twig from the specimen KUN PCLH1-0353 (arrow). 7. Close up of the subulate leaves (arrow in 6), showing adaxial and abaxial surfaces convex (Sc), and apex incurved (Ap), base decurrent (Db). Bar = 5 mm. 9 and 10. Leafy shoots of KUN PCLH1-0344. Bar = 1 cm. 4, 8 and 11. Leafy shoots from Kunming Institute of Botany. Bar = 1 cm. 8. Enlargement of 4, showing surfaces convex (Sc), apex incurved (Ap) and base decurrent (Db). 11. Leafy shoots, arrows indicating the similar part with 9 and 10.

(1968) from Miocene deposits of Rhineland, Germany, were identified based on seed cones and leafy shoots, respectively. These organs probably originated from the same fossil plant and thus likely represented a whole-plant species. Fossils of *Cryptomeria anglica* Boulter (1970) were described based on anatomically preserved leafy shoots from the Neogene of Derbyshire, UK (Boulter, 1970; Boulter and Chaloner, 1970), and Miocene sediments in Iceland (Denk et al., 2005). *Cryptomeria anglica* and *C.* cf. *rhenana* have similar gross morphology and cuticle

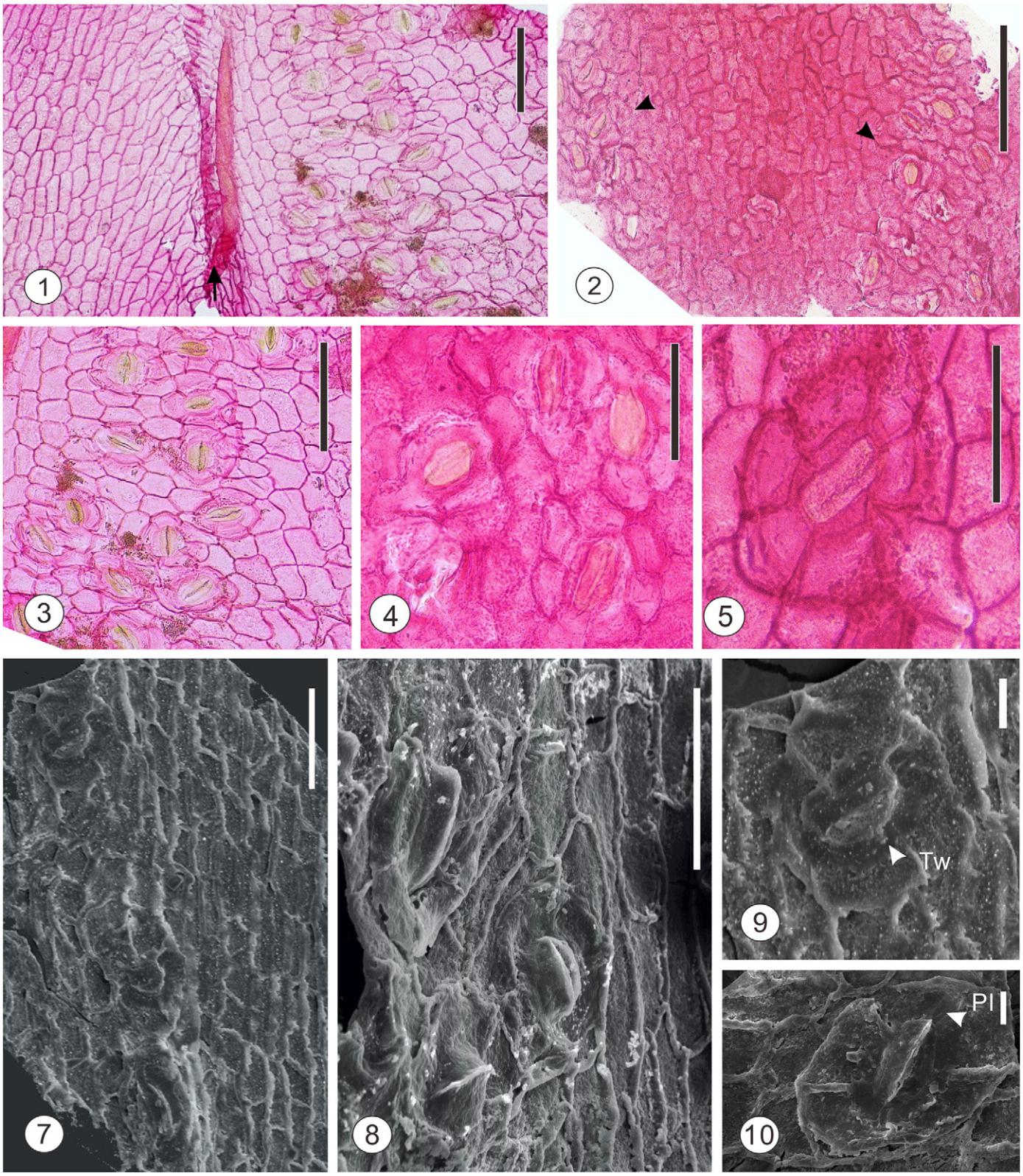

Plate III. Cuticle micromorphology of *Cryptomeria yunnanensis* sp. nov. (1–5 by LM; 7–10 by SEM). 1–3. Showing epidermal cells and stomatal band. Bar = 100 μm. 4 and 5. Stomata monocyclic, densely arranged and irregularly oriented. Bar = 50 μm. 7 and 8. Showing long axes of stoma oblique to midrib. Bar = 100 μm. 9 and 10. Enlargement of stomatal complexes in a stomatal band. Stomata roundish or oval to elongate in shape, with guard cells having distinctly thickened walls (arrow Tw). The thickened walls of guard cells form polar lamellae (arrow Pl). Scale bar = 10 μm.

structures (Denk et al., 2005). Our fossils show similar morphological features to the leafy shoots of *C. anglica* and *C.* cf. *rhenana* but differ from these fossils in cuticular micromorphology (Table 3). The stomata of our fossils are monocyclic (Plate III, 4–9), while *C. anglica* and *C.* cf. *rhenana* possess stomata that are incompletely amphicyclocyclic (Kilpper, 1968; Denk et al., 2005).

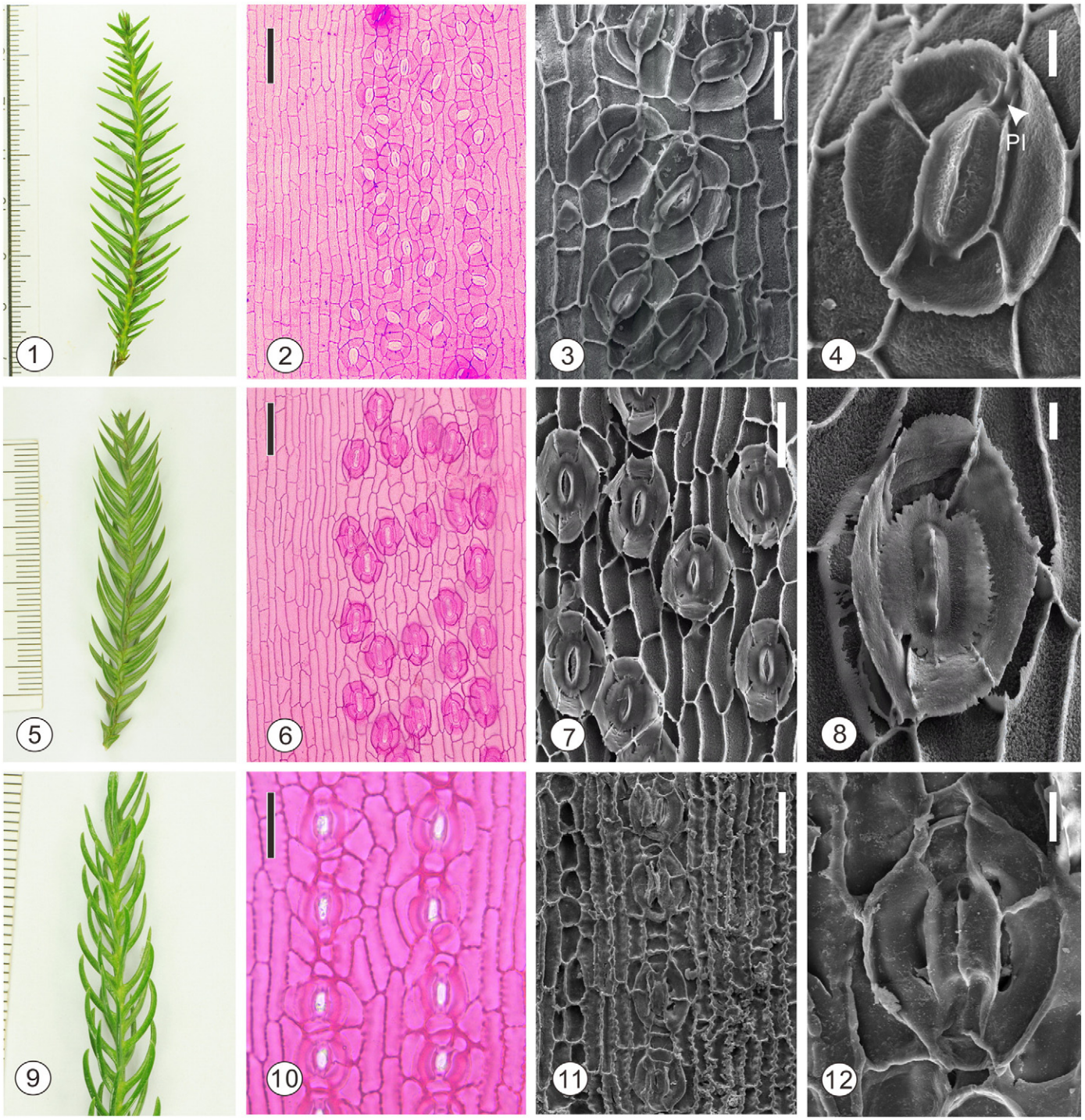

Plate IV. Comparison of leaf morphology and cuticular micromorphology of *Cryptomeria japonica* (1–4), *Taiwania cryptomerioides* (5–8) and *Araucaria cunninghamii* (9–12). 1, 5 and 9. Showing subulate leaves spirally arranged. Leafy shoot collected from Kunming Institute of Botany (1, 5) and Xishuangbanna Tropical Botanical Garden (9). 2–4. Cuticles of *Cryptomeria japonica*. 2. Showing epidermal cells and stomatal bands. Bar = 100 μm. 3. Stomata monocyclic, densely arranged and irregularly oriented, oval to roundish. Bar = 50 μm. 4. Enlargement of the stomatal apparatus. Arrow indicates the thickened walls of guard cells (Pl). Bar = 10 μm. 6–8. Cuticles of *Taiwania cryptomerioides*. 6. Showing epidermal cells and stomatal bands. Bar = 100 μm. 7. Stomata regularly arranged with the long axes of stomata mostly parallel to midvein, rectangular to elongate in shape. Bar = 50 μm. 8. Showing subsidiary cells bordered by thicker peripheral line. Bar = 10 μm. 10–12. Cuticles of *Araucaria cunninghamii*. 10, 11. Showing conspicuous undulated epidermal cells, and regularly arranged stomatal bands. Bar = 50 μm. 12. Inner surface of stomatal apparatus. Bar = 10 μm.

Specimens of *Cryptomeria miyataensis* from the Upper Miocene of Japan (Nishida and Uemura, 1997) differ from our specimens, mainly in the shape and size of leaves, angular divergence of leaves from the axis, and the orientation of stomatal pits. Falcate leaves of *C. miyataensis* are larger and have a wider leaf axis angle. The long axes of their stomata are mostly oriented perpendicular to the midvein compared with the irregular orientation seen in our fossils.

The leaf shape of *Cryptomeria kamtschatica* Chelebaeva (1991), described from the upper Eocene of Russia (Budantsev, 1997; Chelebaeva, 1991), is quite different from our specimens. Leaves of *C. kamtschatica* are falcate and are incurved at the apex. However, the cuticular micromorphology of *C. kamtschatica* is not observable, which prevents further comparison with our fossils. *Cryptomeria protojaponica* Klimova (1975) and *Cryptomeria sichotensis* Pimenov (1984) from the

Table 1
Occurrences of *Cryptomeria* macrofossils in approximate stratigraphic order, respectively.

Species	Age	Locality	Latitude	Longitude	References
C. kamtschatica	Late Eocene	Kamchatka, Russia	55.19	160.83	Chelebaeva (1991); Budantsev (1997)
C. yunnanensis	Rupelian	Yunnan, China	25.14	101.38	This study
C. protojaponica	Oligocene	Primorye, Russia	44.16	132.50	Klimova (1975); Tanai and Uemura (1994)
C. sichotensis	Oligocene	Primorye, Russia	44.16	132.50	Pimenov (1984); Nishida and Uemura (1997)
Cryptomeria sp.	Early Miocene	Joban, Japan	37.00	141.00	Yabe (2008)
Cryptomeria sp.	Early Miocene	Bitterfeld, Germany	51.63	12.35	Jähnichen (1998)
C. miyataensis	Late Miocene	Akita, Japan	39.72	140.10	Nishida and Uemura (1997)
C. rhenana	Early late Miocene	Rhein, Germany	52.28	7.44	Kilpper (1968)
C. cf. *rhenana*	Late Miocene	Rhein, Germany	52.28	7.44	Kilpper (1968)
C. anglica	Late Miocene	La Cerdana, Spain	42.30	2.90	Barrón (1998); Barrón et al. (2014)
C. anglica	Late middle Miocene	Brjánslækur, Iceland	65.51	−23.44	Denk et al. (2005)
C. japonica	Late Miocene	Gruzia	42.63	43.61	Sveshnikova (1953, 1963)
C. anglica	Late Miocene to early Pliocene	Derbyshire, England	53.25	−2.00	Boulter (1970); Boulter and Chaloner (1970)
C. rhenana	Early and middle Pliocene	Northern Italy	45.32	7.61	Martinetto (1995); Martinetto et al. (1997)
C. rhenana	Middle Pliocene	Dunarobba, Italy	42.67	12.45	Martinetto (2001)
C. japonica	Late Pliocene	Osaka, Japan	34.68	135.5	Momohara (1992)
C. japonica	Pliocene	Duab, Abkhazia	43.57	40.38	Kolakovsky (1958)
Cryptomeria sp.	Pliocene	Honshu, Japan	36.45	137.06	Nishida and Uemura (1997)
C. rhenana	Early Pleistocene	Umbria, Italy	43.11	12.39	Martinetto et al. (2017)
Cryptomeria sp.	Pleistocene	Kyushu, Japan	32.52	130.67	Miki (1950); Momohara (2016)

Oligocene of the Primorye region, Russia, were described based on morphological characters and cuticles. The two species largely differ from our fossils in their linear to subulate leaves and the smaller stomatal apparatus (Table 3). *Cryptomeria subulata* was originally described as *Sequoia subulata* Heer (1875). From the images of Sveshnikova (1967, Plate VII, 9, 10), one can see that the helically arranged leaves are lanceolate, spreading, mostly straight, and only some leaves are slightly incurved at the apices (Sveshnikova, 1967). Its affiliation to *Cryptomeria* is not proven by epidermal characters and thus this determination remains doubtful.

The extant species *Cryptomeria japonica* has two varieties, *C. japonica* var. *japonica* and *C. japonica* var. *sinensis* (Fu et al., 1999). The main differences between the two varieties are pollen cone sizes and seed cone scale numbers (Fu et al., 1999), which are not crucial in comparison with our fossils. The extant species primarily differs from our fossils in the shape and size of subulate leaves, the size of epidermal cells, and the arrangement of the stomata (Plates I–III; IV, 1–4; Table 3). Subulate leaves in our fossils are smaller than those in *C. japonica* (Table 3). Moreover, subulate to linear leaves in extant *C. japonica* and *C. japonica fossilis* (Sveshnikova, 1953, 1963) are absent from our fossils. In contrast to *C. japonica*, epidermal cells in the non-stomatal areas of our fossils are smaller and more irregular, and stomata are more irregularly arranged compared to the extant species (Plates III, 1–3; IV, 2–4; Table 3).

In summary, our fossils show macromorphological or cuticular differences from other fossil species assigned to *Cryptomeria* and from the extant *Cryptomeria japonica*. Even though our fossils cannot completely be compared with *C. japonica* because the fossil specimens lack reproductive organs, both species are distinct based on the characters of the leafy shoots. Therefore, we propose a new species, namely *Cryptomeria yunnanensis* W.N. Ding et Z.K. Zhou sp. nov.

4.3. Biogeographic and palaeoecological implications

Fossil records of *Cryptomeria* are confined to Eurasia (Fig. 3; Table 1). During the Paleogene, *Cryptomeria* was present in East Asia; much earlier than it occurred in Europe. The earliest fossil record of *Cryptomeria* is from the upper Eocene of Kamchatka, Russia (Chelebaeva, 1991; Budantsev, 1997). By the Rupelian, *Cryptomeria* appeared in southwestern China, as evidenced by the fossils of *Cryptomeria yunnanensis* sp. nov. from Yunnan. During the Oligocene, the genus was present in Primorye, Russia, with two species, *Cryptomeria protojaponica* and *Cryptomeria sichotensis* (Klimova, 1975; Pimenov, 1984; Tanai and Uemura, 1994). The European fossil records of *Cryptomeria* date back to the Neogene and Quaternary, and the genus occurred frequently in central and southern Europe between the early Miocene and early Pleistocene (Sveshnikova, 1953, 1963; Kolakovsky, 1958; Kilpper, 1968; Boulter,

Table 2
Comparison of leaves and cuticles with *Cryptomeria*.

Genus		*Cryptomeria*	*Taiwania*	*Taxodium*	*Glyptostrobus*	*Araucaria*
Leaves	Shape	LSL, SL	LSL, SL, SLL	LL, LSL or SLL	LL, LSL, SLL	LSL or SL, SLL
	Adaxial and abaxial surfaces convex	Yes	Yes	No	No	Yes
Epidermal cells (between stomatal bands)	Anticlinal walls	Straight	Straight	Straight	Straight	Undulate
	Length (μm)	30.2–88.8	69.8–109.4	63.5–101.9	100.5–162.7	33.0–162.0
	Width (μm)	12.2–20.4	15.5–20.9	20.4–30.2	26.2–37.0	5.0–12.0
	L:W	1.1–6.1	3.7–6.3	2.2–4.6	2.6–6.2	_
Stomata	Type	Monocyclic	Monocyclic	Incompletely amphicyclocytic	Monocyclic	Monocyclic
	Orientation	Oblique	Parallel	Oblique, perpendicular	Parallel (LL, SL); Perpendicular, oblique (SLL)	Parallel, perpendicular, oblique
	Length (μm)	44.3–67.3	49.7–56.9	36–88	41.7–48.7	55–96
	Width (μm)	36.6–56.2	26.7–31.9	28–88	20.2–25.4	41–78
	L:W	1.0–1.6	1.6–2.0	_	1.8–2.2	_
References		This study	LePage (2009)	Kunzmann et al. (2009)	Ma et al. (2004a)	Stockey and Taylor (1978); Stockey and Ko (1986)

LL: linear leaves; LSL: linear-subulate leaves; SL: subulate leaves; SLL: scalelike leaves.

Table 3
Morphological characteristics, age and distribution of *Cryptomeria* species.

Character	*C. yunnanensis*	*C. rhenana*	*C.*cf. *rhenana*	*C. anglica*	*C. miyataensis*	*C. protojaponica*	*C. sichotensis*	*C. kamtschatica*	*C. japonica*
Leaves									
Shape	Subulate	_	Subulate	Falcate	Falcate	Linear-subulate	Linear-subulate	Subulate	Linear-subulate; subulate
Length (mm)	1.6–6.2	_	2.4–4.6	4.5–9.3	5.6–8.4	3–5	5.5–6.0	_	4.0–20.0
Width (mm)	0.8–2.1	_	1.3–1.8	0.8–1.9	1.0–2.2	0.5–0.6	1.2–1.5	_	0.8–1.2
Length/width	1.5–4.4	_	1.8–2.8	2.9–7.2	3.8–7.1	_	_	_	1.8–9.8
Apex	Acute	_	Blunt	Blunt	Acute	Acute	Blunt	Blunt	Blunt or acute
	Straight or incurved	_	Straight or incurved	Incurved	Incurved	Incurved	Incurved	Incurved	Straight or incurved
Base	Long decurrent	_	Long decurrent	Long decurrent	Long decurrent	Long decurrent	Long decurrent	Long decurrent	Long decurrent
Midrib	Convex	_	Convex	Convex	Convex	Convex	Convex	Convex	Convex
Epidermal cell shape	Elongate, rectangular, quadrangular or spindle-shaped	Oblong, elongate, rectangular	Oblong, elongate to rectangular	_	Oblong, rectangular to elongate	Rectangular to elongate or polygonal	Rectangular to elongate	_	Oblong, rectangular to elongate
Length (μm)	27.5–63.2	33.4–76.5	32.5–68.1	_	9.9–20.5	19–66	44–78	_	30.2–88.8
Width (μm)	10.0–27.3	12.7–24.2	12.4–21.1	_	6.4–11.8	9.9–29.7	10–14	_	12.2–20.4
Length/width	0.6–5.3	1.4–6.8	1.8–3.3	_	0.8–2.7	_	_	_	1.1–6.1
Stoma									
Shape	Oval to roundish	Quadrangular, spherical	Quadrangular, spherical	Oval to roundish	Quadrangular, spherical	Oval to roundish	Oval to roundish	_	Rectangular, spindle-shaped
Type	Monocyclic	Incompletely amphicyclocyclic	Incompletely amphicyclocyclic	Incompletely amphicyclocyclic	Monocyclic	Monocyclic	Monocyclic	_	Monocyclic
Length (μm)	40–73.4	40.2–65.9	46.4–62.4	46.6–53.7	24.5–35.0	23.1	20–30	_	44.3–67.3
Width (μm)	34.2–63.5	39.1–63.3	33.9–50.4	36.9–40.0	18.3–24.8	_	10–16	_	36.6–56.2
Length/width	0.7–1.9	1.0–1.3	1.1–1.6	1.2–1.4	1.0–1.5	_	_	_	1.0–1.6
Subsidiary cells	10.2–24.7	7.1–20.5	7.6–15.7	_	5.1–10.3	_	_	_	9.0–21.0
Stoma orientation	Long axis randomly oblique to midvein	Long axis mostly oblique or perpendicular to midvein	Long axis mostly oblique or perpendicular to midvein	Long axis mostly oblique or perpendicular to midvein	Long axis mostly perpendicular to midvein	Long axis mostly oblique to midvein	Long axis mostly oblique to midvein	_	Long axis randomly oblique to midvein
Age	Rupelian	Miocene to Pliocene	Late Miocene	Miocene to Pliocene	Miocene	Oligocene	Oligocene	Late Eocene	Extant
Distribution	China	Germany, Italy	Germany	England, Iceland, Spain	Japan	Russia	Russia	Russia	China, Japan
References	This study	Kilpper (1968); Martinetto (1995); Martinetto et al. (1997); Martinetto (2001)	Kilpper (1968)	Barrón (1998); Boulter (1970); Barrón et al. (2014); Denk et al. (2005)	Nishida and Uemura (1997)	Klimova (1975)	Pimenov (1984)	Chelebaeva (1991); Budantsev (1997)	This study

1970; Boulter and Chaloner, 1970; Martinetto, 1995; Martinetto et al., 1997; Barrón, 1998; Jähnichen, 1998; Martinetto, 2001; Denk et al., 2005; Barrón et al., 2014; Martinetto et al., 2017).

Palaeoclimatic reconstructions in Europe based on palaeobotanical records indicate a humid and subtropical to temperate climate during the early and middle Miocene (Utescher et al., 2000; Mosbrugger et al., 2005; Utescher et al., 2009), climatic conditions which may have been quite suitable for *Cryptomeria*. Taking *Cryptomeria* fossils from the middle Miocene in Saxony as an example, fossil remains (wood, leaves and dispersed leaf cuticles) were recovered from peat swamp deposits in coastal plains where they were associated with *Sciadopitys tertiaria* in raised bog swamp forest (Dolezych and Schneider, 2006). Raised bogs in paralic swamps can be only developed under humid conditions because water supply exclusively comes from precipitation (Dolezych and Schneider, 2006). Subtropical temperatures are considered for this time interval based on co-existing fossil plant assemblages in mesic environments including Symplocaceae, Mastixiaceae, trigonobalanoid Fagaceae, Lauraceae and others (Mai, 2000). By the end of the Pliocene, a drastic decrease in precipitation occurred across Europe associated with a significant decrease in temperatures (Mosbrugger et al., 2005). The genus was exclusively present in some refuge areas in the Mediterranean but finally became extinct in Europe during the Pleistocene.

In contrast to the history in Europe, many Cenozoic relic genera, including *Cryptomeria*, survived in East Asia in relatively complex topographies in the lower latitudes (Huang et al., 2015). Currently, *Cryptomeria japonica* naturally occurs in mixed deciduous and/or evergreen broadleaved forests in Japan and along the Yangtze River, central southern China (Tsukada, 1982; Nishida and Uemura, 1997; Fu et al., 1999; Da et al., 2009). *Cryptomeria japonica* thrives in humid areas with abundant precipitation in both cool- and warm-temperate zones. In Japan, *Cryptomeria japonica* grows in areas with a mean annual temperature between 10.0 °C and 14.0 °C (Tsukada, 1982; Takahara and Kitagawa, 2000). In relation to precipitation, the natural distribution of *C. japonica* is restricted to areas with a mean annual precipitation being not less than 1200 mm (Tsukada, 1967; Tsukada, 1986; Wang et al., 2007). Overall, humid climatic conditions are probably an essential physical factor that enables *Cryptomeria* to exist (Kaizuka, 1980; Nishida and Uemura, 1997; Yabe, 2008).

Relic areas in central southern China provide warm and moist conditions similar to those in Japan. In these areas, Fujian (Nanping), Jiangxi (Mt. Lu shan), and Zhejiang (Mt. Tianmu shan) (Fig. 3), today's observed

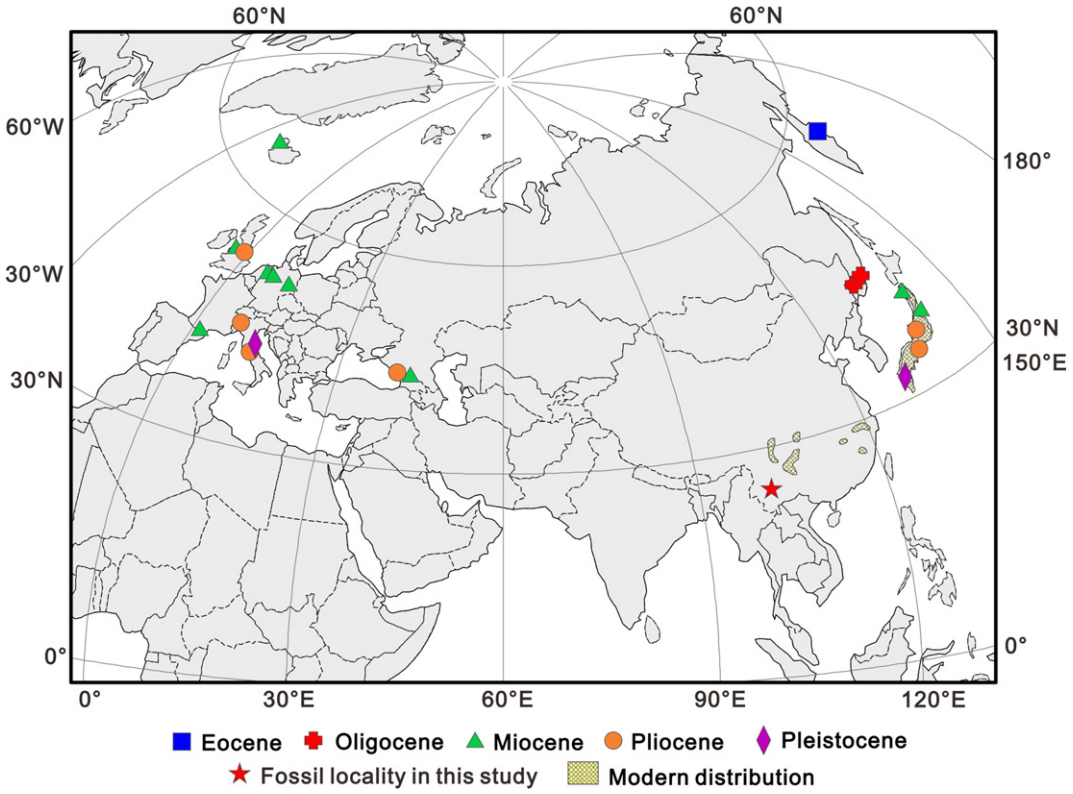

Fig. 3. Modern distribution ranges and fossil record of *Cryptomeria* based on leafy remains. Detailed information on each fossil record is listed in Table 1.

mean annual temperatures range between 16.0 °C and 19.0 °C and mean annual precipitations between 1500 mm and 2000 mm (Fu et al., 1999; Ma et al., 2007; Wang et al., 2007). However, the location of the Rupelian native stand in central Yunnan nowadays experiences a subtropical monsoon climate with a mean annual temperature of 14.8 °C and a mean annual precipitation of 841.1 mm (Yunnan Meteorological Bureau, 1983). The humidity of Lühe is significantly lower during the dry season (October to April) compared with the ecological requirements in both the modern natural distribution areas and well-studied fossil localities bearing associations with *Cryptomeria* (e.g., Dolezych and Schneider, 2006). Therefore, insufficient annual precipitation and reduced humidity might have been the cause of the demise of *Cryptomeria* in central Yunnan. In short, deduced from modern and fossil occurrences of *Cryptomeria*, we conclude that palaeoclimate change, in particular, the decrease in precipitation in several parts of Eurasia, are crucial factors for shaping the present-day relic distribution pattern of *Cryptomeria* in East Asia.

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References

Barrón, E., 1998. Estudio paleobotánico del afloramiento vallesiense (Neógeno) del torrente de Vilella (La Cerdaña, Lérida, España): aspectos tafonómicos y paleoecológicos. Boletín de la Real Sociedad Española de Historia Natural. Sección Geol. 94, 41–61 (in Spanish, with English abstract).

Barrón, E., Postigo-Mijarra, J.M., Diéguez, C., 2014. The late Miocene macroflora of the La Cerdanya Basin (Eastern Pirenees, Spain): towards a Synthesis. Palaeontogr. Abt. B 291 (1–6), 85–129.

Boulter, M., 1970. *Cryptomeria* – a significant component of the European Tertiary. Paläontologische Abhandlungen B. Vol. III, pp. 279–287 (Part 3/4).

Boulter, M.C., Chaloner, W.G., 1970. Neogene fossil plants from Derbyshire (England). Rev. Palaeobot. Palynol. 10 (1), 61–78.

Budantsev, L.Y., 1997. Late Eocene flora of western Kamchatka. Russian Academy of Sciences, Proceedings of Komarov Botanical Institute. 19, pp. 3–115 (in Russian, with English summary).

Chelebaeva, A.I., 1991. Floristic characteristics of the Snatol'j and Kowchinsk horizons. Trans. Geol. Inst. Acad. Sci. USSR 467 (49–63), 76–119 (in Russian).

Da, L.J., Kang, M.M., Song, K., Shang, K.K., Yang, Y.C., Xia, A.M., Qi, Y.F., 2009. Altitudinal zonation of human–disturbed vegetation on Mt. Tianmu, eastern China. Ecol. Res. 24 (6), 1287–1299.

Denk, T., Grímsson, F., Kvaček, Z., 2005. The Miocene floras of Iceland and their significance for late Cainozoic North Atlantic biogeography. Bot. J. Linn. Soc. 149, 369–417.

Dolezych, M., Schneider, W., 2006. Xylotomie und feinstratigraphisch-fazielle Zuordnung von inkohlten Hölzern und dispersen Kutikulen aus dem 2. Lausitzer Flöz (Miozän) im Tagebau Welzow. Z. Geol. Wiss. 34 (3–4), 165–259 (in German).

Fu, L.G., Yu, Y.F., Mill, R.R., 1999. Taxodiaceae. In: Wu, Z.Y., Raven, P. (Eds.), Flora of China. Science Press, Beijing, pp. 281–293.

Heer, O., 1875. Die Kreideflora der Arctischen Zone. Flora Fossilis Arctica, Bd. II1. p. 102 (in German).

Huang, Y.J., Jacques, F.M.B., Su, T., Ferguson, D.K., Tang, H., Chen, W.Y., Zhou, Z.K., 2015. Distribution of Cenozoic plant relicts in China explained by drought in dry season. Sci Rep 5, 14212.

Jähnichen, H., 1998. Erstnachweis von *Taiwania*, *Cryptomeria* und *Liquidambar* aus dem Bitterfelder und baltischen Bernstein. Fossil Rec. 1, 167–177 (in German).

Kaizuka, S., 1980. Late Cenozoic palaeogeography of Japan. GeoJournal 4, 101–109.

Kerp, H., 1990. The study of fossil gymnosperms by means of cuticular analysis. PALAIOS 5 (6), 548–569.

Kilpper, K., 1968. Koniferen aus den Tertiären Deckschichten des Niederrheinischen Hauptflözes, 3. Taxodiaceae und Cupressaceae. Palaeontographica Abteilung B Band 124 Lieferung. 4–6 pp. 102–111 (in German).

Klimova, R., 1975. Miocene conifers from Rettikhovka. Proceedings of the Institute of Biology and Pedology, Far Eastern Scientific Centre, Academy of Sciences of the USSR, New Series 27, pp. 84–92 (in Russian, with English abstract).

Kolakovsky, A.A., 1958. The first addition to the Pliocene flora of Duab. Trudy Sukhumskogo Botanicheskogo Sada. 11, pp. 311–397 (in Russian, with English summary).
Kunzmann, L., Kvaček, Z., Mai, D.H., Walther, H., 2009. The genus *Taxodium* (Cupressaceae) in the Palaeogene and Neogene of Central Europe. Rev. Palaeobot. Palynol. 153, 153–183.
LePage, B.A., 2009. Earliest occurrence of *Taiwania* (Cupressaceae) from the early Cretaceous of Alaska: Evolution, biogeography, and paleoecology. Proc. Acad. Natl. Sci. Phila. 158 (1), 129–158.
Linnemann, U., Su, T., Kunzmann, L., Spicer, R.A., Ding, W.N., Spicer, T.E.V., Zieger, J., Hofmann, M., Moraweck, K., Gärtner, A., Gerdes, A., Marko, L., Zhang, S.T., Li, S.F., Tang, H., Huang, J., Mulch, A., Mosbrugger, V., Zhou, Z.K. 2017. New U-Pb dates show a Paleogene origin for the modern Asian biodiversity 'Hotspots'. Geology (Submitted for publication).
Ma, Q.W., Li, C.S., Li, F.L., Vickulin, S.V., 2004a. Epidermal structures and stomatal parameters of Chinese endemic *Glyptostrobus pensilis* (Taxodiaceae). Bot. J. Linn. Soc. 146, 153–162.
Ma, Q.W., Li, F.L., Li, C.S., 2004b. Leaf epidermal structure and stomatal parameters of the genus *Taxodium* (Taxodiaceae). Acta Phytotaxonomica Sin. 43 (6), 517–525.
Ma, Q.W., Li, F.L., Li, C.S., 2005. The coast redwoods (*Sequoia*, Taxodiaceae) from the Eocene of Heilongjiang and the Miocene of Yunnan, China. Rev. Palaeobot. Palynol. 135 (3), 117–129.
Ma, Q.W., Li, C.S., Li, F.L., 2007. Epidermal structures of *Cryptomeria japonic*a and implications to the fossil record. Acta Palaeobot. 47, 281–289.
Mai, D.H., 1997. Die oberoligozänen Floren am Nordrand der sächsischen Lausitz. Palaeontographica Abteilung B Band 244 Lieferung 1–6. pp. 1–124 (in German).
Mai, D.H., 2000. Die untermiozänen Floren aus der Spremberger Folge und dem 2. Flözhorizont der Lausitz, Teil IV: Fundstellen und Paläobiologie. Palaeontogr. Abt. B 254, 65–176 (in German).
Mai, D.H., Walther, H., 1988. Die pliozänen Floren von Thüringen, Deutsche Demokratische Republik. Quartärpaläontologie 7, 55–297 (in German).
Manchester, S.R., Chen, Z.D., Lu, A.M., Uemura, K., 2009. Eastern Asian endemic seed plant genera and their paleogeographic history throughout the Northern Hemisphere. J. Syst. Evol. 47, 1–42.
Martinetto, E., 1995. Chronological and Paleoenvironmental Meaning of Plant Macrofossils in the Stratigraphical Framing of the "Villafranchiano" Unit in Some Districts of the Piemonte Region (NW Italy). (PhD Thesis). Dipartimento di Scienze della Terra, Universita degli Studi di Torino (in Italian, with English summary).
Martinetto, E., 2001. The role of central Italy as a centre of refuge for thermophilous plants in the late Cenozoic. Acta Palaeobot. 41, 299–319.
Martinetto, E., Pavia, G., Bertoldi, R., 1997. Fruit and seed floras rich in exotic and subtropical elements from two Lower Pliocene successions of Italy. Mededelingen Nederlands Instituut voor Toegepaste Geowetenschappen TNO. 58, pp. 237–244.
Martinetto, E., Momohara, A., Bizzarri, R., Baldanza, A., Delfino, M., Esu, D., Sardella, R., 2017. Late persistence and deterministic extinction of "humid thermophilous plant taxa of East Asian affinity" (HUTEA) in southern Europe. Palaeogeogr. Palaeoclimatol. Palaeoecol. 467, 211–231.
Miki, S., 1950. Taxodiaceae of Japan, with special reference to its remains. J. Inst. Polytech. Osaka City Univ. Ser. D 13, 65–85.
Milne, R.I., Abbott, R.J., 2002. The origin and evolution of tertiary relict floras. Adv. Bot. Res. 38, 281–314.
Momohara, A., 1992. Late Pliocene plant biostratigraphy of the lowermost part of the Osaka Group, southwest Japan, with reference to extinction of plants. Quat. Res. (Daiyonki-Kenkyu) 31, 77–89.
Momohara, A., 2016. Stages of major floral change in Japan based on macrofossil evidence and their connection to climate and geomorphological changes since the Pliocene. Quat. Int. 397, 92–105.
Mosbrugger, V., Utescher, T., Dilcher, D., 2005. Cenozoic continental climatic evolution of Central Europe. Proc. Natl. Acad. Sci. U. S. A. 102 (42), 14964–14969.
Nishida, H., Uemura, K., 1997. Phytogeographic history of Taxodiaceae and importance of preserving mixed broad–leaved deciduous/evergreen forest. Tropics 6, 413–420.
Pimenov, G., 1984. New information on *Cryptomeria* from the Miocene epoch of the far-east. Paleontol. Zh. 1, 80–85.
Stockey, R.A., Ko, H., 1986. Cuticle micromorphology of *Araucaria* de Jussieu. Bot. Gaz. 147 (4), 508–548.
Stockey, R.A., Taylor, T.N., 1978. Cuticular features and epidermal patterns in the genus *Araucaria* de Jussieu. Bot. Gaz. 139 (4), 490–498.
Sveshnikova, I.N., 1953. The finding of the genus *Cryptomeria* D. Don in Gruzia. Doklady Acad. Sci. USSR New Ser. 92 (2), 417–419 (in Russian).
Sveshnikova, I.N., 1963. Atlas and key for the identification of the living and fossil Sciadopityaceae and Taxodiaceae based on the structure of the leaf epiderm. Paleobotanika 4 (8), 225–226 (in Russian, with English summary).
Sveshnikova, I.N., 1967. Late Cretaceous coniferae of the U.S.S.R. 1. Fossil coniferae of the Viliuyian depression. Transactions of the Botanical Institute of V.L. Komarov, AN SSSR. Paleobotanika 6, 196 (in Russian, with English summary).
Takahara, H., Kitagawa, H., 2000. Vegetation and climate history since the last interglacial in Kurota Lowland, western Japan. Palaeogeogr. Palaeoclimatol. Palaeoecol. 155 (1), 123–134.
Tanai, T., Uemura, K., 1994. Lobed oak leaves from the Tertiary of East Asia with special reference to the oak phytogeography of the Northern Hemisphere. Trans. Proc. Palaeontol. Soc. Japan New Ser. 173, 343–356.
Tsukada, M., 1967. Pollen succession, absolute pollen frequency, and recurrence in Central Japan. Am. J. Bot. 54, 821–831.
Tsukada, M., 1982. *Cryptomeria japonica*: glacial refugia and late–glacial and postglacial migration. Ecology 63 (4), 1091–1105.
Tsukada, M., 1986. Altitudinal and latitudinal migration of *Cryptomeria japonica* for the past 20,000 years in Japan. Quat. Res. 26 (1), 135–152.
Utescher, T., Mosbrugger, V., Ashraf, A.R., 2000. Terrestrial climate evolution in northwest Germany over the last 25 million years. PALAIOS 15 (5), 430–449.
Utescher, T., Mosbrugger, V., Ivanov, D., Dilcher, D., 2009. Present-day climatic equivalents of European Cenozoic climates. Earth Planet. Sci. Lett. 284, 544–552.
Wang, J., Liu, J., Huang, Y.Q., Yang, J.H., 2007. The origin and natural distribution of *Cryptomeria*. J. Sichuan For. Sci. Technol. 28 (4), 92–94 (in Chinese, with English abstract).
Wissink, G.K., Hoke, G.D., Garzione, C.N., Jing, L.Z., 2016. Temporal and spatial patterns of sediment routing across the southeast margin of the Tibetan Plateau: insights from detrital zircon. Tectonics 35, 2538–2563.
Xing, Y.W., Gandolfo, M.A., Onstein, R.E., Cantrill, D.J., Jacobs, B.F., Jordan, G.J., Vikulin, S.V., 2016. Testing the biases in the rich Cenozoic angiosperm macrofossil record. Int. J. Plant Sci. 177 (4), 371–388.
Xu, J.X., Wang, Y.F., Li, C.S., Ferguson, D.K., 2008. Late Miocene vegetation and climate of the Lühe region in Yunnan, southwestern China. Rev. Palaeobot. Palynol. 148, 36–59.
Yabe, A., 2008. Early Miocene terrestrial climate inferred from plant megafossil assemblages of the Joban and Soma areas, Northeast Honshu, Japan. Bull. Geol. Surv. Jpn 59, 397–413.
Yi, T.M., Li, C.S., Xu, J.X., 2003. Late Miocene woods of Taxodiaceae from Yunnan, China. Acta Bot. Sin. 45, 384–389.
Yunnan Meteorological Bureau, 1983. Agricultural Climatic Data of Yunnan Province. Yunnan People's Publishing House, Kunming, China (in Chinese).
Zhang, Z.Y., 1996. Multiple classification and correlation of the stratigraphy in China. Stratigraphy (Lithostratic) of Yunnan Province. China University of Geosciences Press, Wuhan, China, pp. 53–328 (in Chinese).
Zhang, Y.L., Ferguson, D.K., Ablaev, A.G., Wang, Y.F., Li, C.S., Xie, L., 2007. *Equisetum* cf. *pratense* (Equisetaceae) from the Miocene of Yunnan in southwestern China and its paleoecological implications. Int. J. Plant Sci. 168 (3), 351–359.